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THE PROGRESSION OF LIFE IN THE SEA[1]

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THE method we usually follow in the ordinary course of zoological work is to make first, with the unaided eye, a general examination of the animal that interests us, and then study in detail its separate parts with a simple lens, with a low power of the microscope, with gradually increasing powers, until, finally, minute portions are examined with the highest oil-immersion lens. The successful research worker is generally one who, whilst carrying to the utmost limit he can achieve his search into detail, maintains as by instinct a true sense of proportion and holds firmly to the idea of the organism as a whole.

In discussing the living organisms of the sea I shall try to follow a similar plan, thinking of the life of the sea as a whole, built up of individual plants and animals, each in intimate relation with its surroundings, and all interdependent among themselves. But even this is not enough, for we must take still a wider view and keep in mind not only the life of the waters, but that also of the land and of the air, for both, as we shall see, have a bearing on our theme. Deep oceans, coastal waters, shallow seas, rivers and lakes, continents and islands, all play their part in one scheme of organic life—life which had, it seems, one origin, and, notwithstanding migrations and transmigrations from water to land, from land to air, and from land and air back again to the water, remains one closely interrelated whole.

[1] Address of the President of the Section of Zoology of the British Association for the Advancement of Science, Hull, September, 1922.

Both Brandt[2] and Gran[3] have recently emphasized the fact that it is in the coastal waters and shallow seas, which receive much drainage from the land, that plant and animal life are most abundant, the more open oceans far from land being relatively barren; as Schütt puts it, the pure blue of the oceans is the desert color of the seas. This increased production in the coastal waters is due principally to the presence of nitrogen compounds and compounds of phosphorus derived from terrestrial life. From forest, moor and fen, wherever water trickles, the life of the land sends its infinitesimal quota of these essential foodstuffs to fertilize the sea.

When, however, we go back to the beginning of things, we shall probably be right if we say that any influence of terrestrial life upon life in the sea must be left out of account. Different views are still held as to where life in the world had its origin, but no one questions that it began in close connection with water. That it began in the sea, where the necessary elements were present in appropriate concentrations and in an ionized state, is an idea which appeals to many with increasing force the more closely it is examined. This view has been developed recently by Church[4] in his memoir on "The Building of an Autotrophic Flagellate," in which he boldly attempts to trace the progression from the inorganic elements present in sea-water to the unicellular flagellate in the plankton phase, floating freely in the water. The autotrophic flagellate, manufacturing its own food, he regards as the starting-point from which all other organisms, both plants and animals, have sprung. To understand the first step in this progression, the passage from the dead inorganic to the living organic remains, as it has always been, one of the great goals of science, not of biological science alone, but of all science. Recent research has, I think, thrown much light on the fundamental problems involved. In a paper published last year, Baly,

2 *Wissensch. Meeresunters.* Kiel, 18, 1916–20, p. 187.

3 *Bull. Planktonique.* Cons. Internat., 1912 (1915).

4 *Biological Memoirs I.* Oxford, 1919.

Heilbron, and Barker,[5] extending and correcting previous work by Benjamin Moore and Webster,[6] have shown that light of very short wave-length ($\lambda = 200\, \mu\mu$), obtained from a mercury-vapor lamp, acting upon water and carbon dioxide alone, is capable of producing formaldehyde, with liberation of free oxygen. Light of a somewhat longer wave-length ($\lambda = 290\, \mu\mu$) causes the molecules of formaldehyde to unite or polymerize to form simple sugars, six molecules of formaldehyde, for example, uniting to form hexose. The arresting fact brought out in these researches is that the reactions take place, under the influence of light of appropriate wave-lengths, without the help of any catalyst, either organic or inorganic. Where a source of light is used which furnishes rays of many wave-lengths, the simple reaction of the formation of formaldehyde is masked by the immediate condensation of the formaldehyde to sugar, but this formation of sugar can be prevented by adding to the solution a substance which absorbs the longer wave-lengths, so that only the short ones which produce formaldehyde are able to act.

When the formation of sugars is postulated, the introduction of nitrogen into the organic molecule offers little theoretical difficulty; for not only has Moore[7] shown that nitrates are converted into the more chemically active nitrites under the influence of light of short wave-length, but he maintains that marine algæ, as well as other green plants, can under the same influence assimilate free nitrogen from the air. Baly[8] also has succeeded in bringing about the union of nitrites with active formaldehyde in ordinary test-tubes by subjecting the mixture to the light of a quartz-mercury lamp.

It will be admitted that these three reactions: (1) the

[5] *Journ. Chem. Soc.*, London, Vols. 119 and 120, 1921, p. 1025. *Nature*, Vol. 109, 1922, p. 344.

[6] *Proc. Roy. Soc.* B., Vol. 87, p. 163 (1913), p. 556 (1914); Vol. 90, p. 168 (1918).

[7] *Proc. Roy. Soc.* B., Vol. 90, p. 158 (1918); Vol. 92, p. 51 (1921).

[8] Baly, Heilbron and Hudson, *Journ. Chem. Soc.*, London, Vols. 121 and 122, 1922, p. 1078.

formation of formaldehyde, H.CO.H, from carbonic acid, OH.CO.OH, with liberation of free oxygen, or, to put it more simply, the direct union of the carbon atom of CO_2 with a hydrogen atom of H_2O; (2) the formation of sugars from formaldehyde, and (3) the formation from nitrites and formaldehyde of nitrogenous organic substances, are the most fundamental and characteristic reactions of organic life. It is true that light of such short wave-lengths ($\lambda = 200\ \mu\mu$) as were required in Baly's experiments to synthesize formaldehyde does not occur in sunlight as it reaches the earth to-day; but, as we shall see later, the same author has shown that, in the presence of certain substances known as photocatalysts, the reaction can be brought about by ordinary visible light; and from Moore and Webster's work it appears that colloidal hydroxides of uranium and of iron are suitable photocatalysts for the purpose.

If these results of the pure chemist are justified, they go far towards bridging the gap which has separated the inorganic from the organic, and make it not too presumptuous to hazard the old guess that even to-day it is possible that organic matter may be produced in the sea and other natural waters without the intervention of living organisms. We may note here, too, that if we take account of only the most accurate and adequately careful work, the actual experimental evidence at the present time requires the presence of a certain amount of organic matter in the culture medium or environment before the healthy growth of even the simplest vegetable organism can take place. This was illustrated in some experiments made by myself some years ago when attempting to grow a marine diatom, *Thalassiosira gravida,* in artificial sea-water made up from the purest chemicals obtainable dissolved in twice-distilled water. Even after nutritive salts, in the form of nitrates and phosphates, had been added, little or no growth of the diatom occurred. But if as little as 1 per cent. of natural sea-water were added, excellent cultures resulted, in which the growth was as healthy and vigorous as I was able to obtain when natural sea-water was

used entirely as the basis of the culture medium. There was clearly some substance essential to healthy growth contained in the 1 per cent. of natural sea-water, and from further experiments it became practically certain that it was an organic substance. When, for instance, the natural sea-water was evaporated to dryness, the residue slightly heated and redissolved in distilled water, 1 per cent. of this solution added to the artificial culture medium was as potent in producing growth of the diatom as the original natural sea-water had been. When, on the other hand, the residue after evaporation was well roasted at a dull red heat and redissolved in distilled water, the addition of this solution to the artificial culture medium produced no effect and growth did not take place. Growth could also be stimulated by boiling a small fragment of green seaweed (*Ulva*) in the artificial culture medium, the weed being removed before inoculation with the diatom. All this points to the necessity for the presence of some kind of organic matter in the solution before growth can take place. One must not dogmatize, however, for there are many pitfalls in the experimental work and the necessary degree of accuracy is difficult to attain. My own experience of these difficulties culminated when I discovered, covering the bottom of my stock bottle of distilled water—water which had been carefully redistilled from bichromate of potash and sulphuric acid in all-glass apparatus—a healthy growth of mold.

Let us then assume that we are allowed to postulate in primitive sea-water or other natural water organic compounds formed by the energy of light vibrations from ions present in the water, and see how we may proceed to picture the building up of elementary organisms. Without doubt the evolutionary step is a long and elaborate one, for even the simplest living organism is already highly complex both in structure and in function. As the molecules grew more complex by the progressive linkage of the carbon atoms of newly formed carbohydrate and nitrogenous groups, we must suppose that the organic substance, for purely physical reasons, assumed

the colloidal state, and at the same time its surface-tension became somewhat different from that of the surrounding water. With the assumption of the colloidal state, the electric charges on the colloidal particles would produce the effect of adsorption and fresh ions would be attracted from the surrounding medium, producing a kind of growth entirely physical in character. We thus arrive at the conception of a mass of colloidal plasma differing in surface-tension from the water and increasing in size by two processes, the one chemical, due to linkage of carbon atoms; the other physical, brought about by the adsorption of ions by the colloidal particles.

The difference of surface-tension would tend to make the surface a minimum and the shape of the mass spherical. On the other hand, maximum growth would demand maximum exchange with the surrounding medium, and hence maximum surface. From the antagonism of these two factors, surface-tension and growth, there would follow, firstly, the breaking up of the mass into minute particles upon the slightest agitation, and, secondly, changes of form wherever growth involved local alterations of surface-tension, which changes of form would represent the first indication of the property of contractility.

So far we have considered only the process of the building up of the elementary plasmic particles, the anabolic process. Church, whose memoir already referred to I am now closely following, points out that these anabolic operations must from the beginning have been subject to the alternations of day and night, for during the night the supply of external energy is removed. "If during the night," he asks, "the machine runs down, to what extent may it be possible so to delay the onset of molecular finality that some reaction may continue, at a lower rate, until the succeeding day?" And his answer is: "The successful solution of this problem is defined physiologically by the introduction of the conception '*katabolism,*' as implying that energy derived from the 'breaking down' of the plasma itself . . . may be regarded as a 'secondary engine,' functional in the absence

of light, and evolved as a last resort in failing plasma." Katabolism persists as the ultimate mechanism in the physiology of animal as contrasted with plant life, but if the suggestion just quoted is sound, it originated, as the first "adaptation" of the organism, to meet the factor of recurring night and day. That the problem was successfully solved we know, but as to the mechanism of its solution we have no key. It is at this point again, to use Church's words, that the "plasma, previously within the connotation of chemical proteid matter, becomes an autotrophic, increasingly self-regulated, and so far individualized entity, to which the term 'life' is applied."

The elementary plasma is thus now fairly launched as an individual living organism, and the great fundamental problems of biology—memory, heredity, variation, adaptation—face us at each step of our further progress. We see in broad outline the conditions the advancing organism had to meet, we see the means by which those conditions were in fact met, we know that only those individuals survived which were able to meet them. Further than this we, the biologists of to-day, have not advanced. The younger generation will pursue the quest, and, with patient effort, much that now lies hidden will grow clear.

The differentiation of the growing particles of plasma into definite layers, which followed, seems natural; first the external layer, in molecular contact with the surrounding water, from which it receives substances from outside in the form of ions, and to which it itself gives off ions; beneath this the autotrophic layer to which light penetrates, and in which, under the influence of the light, new organic substance is built up; in the center a layer to which light no longer penetrates. This central region, the nucleus, depends entirely on the peripheral layers for its own nutrition, and becomes itself concerned only with katabolic processes, those processes of the organism which depend upon the breaking down, and not the building up, of organic substance.

At an early stage in the development of the individual organism the spherical shape, which the organic plasma

was compelled to assume under the influence of surface-tension, underwent an important modification, the effect of which has impressed itself upon all later developments. A spherical organism floating in the water and growing under the direct influence of light would obviously grow more rapidly on the upper side, where the light first strikes it, than it would on the lower side away from the light. There followed, therefore, an elongation of the sphere in the vertical direction, and the definite establishment of an anterior end, the upper end which lay towards the light and at which the most vigorous growth took place. In this way there was established a definite polarity, which has persisted in all higher organisms, a distinction between an anterior and a posterior end. With the concentration of organic substance which took the form of nucleus and reserve food supply, the specific gravity of the plasma would become greater than that of the surrounding water and the organism would tend to sink. The necessity, therefore, arose for some means of keeping it near the surface, that it might continue to grow under the influence of light. The response to this need, however it was attained, came in the development of an anterior flagellum. This we may regard as an elongation in the direction of the light of a contractile portion of the external layer, moving rhythmically, which by its movement counteracted the action of gravity, and acting as a tractor drew the primitive flagellate upwards towards the surface layers, into a position where further growth was possible. That this speculation of Church's represents what was actually accomplished, even though it does not make clear the means by which it was brought about, is shown by the interesting researches of Wager[9] on the rise and fall of the more highly organized flagellate *Euglena*. *Euglena* is a somewhat pear-shaped flagellate, the tapering end being anterior and provided with a single flagellum, which acts as a tractor drawing the organism towards the light. The

[9] *Phil. Trans. Roy. Soc.*, Vol. 201, 1911; and *Science Progress*, Vol. vi, October, 1911, p. 298.

posterior end carries the nucleus and most of the chlorophyll and food reserves. The whole organism has a specific gravity of 1.016, being slightly heavier than the fresh water in which it lives. When dead, or when the flagellum is not moving, it takes up, under the action of gravity alone, a vertical position in the water, with the pointed anterior end uppermost, and the heavier, rounded, posterior end below, and sinks gradually to the bottom.

In a very crowded culture a curious phenomenon is seen, because the organisms tend to aggregate into clusters beneath the surface film, and when they are crowded together in these clusters the flagella cease to work. This makes the whole cluster sink to the bottom under the action of gravity. When the bottom is reached the individuals are spread out by the action of the downward current, and, when they are sufficiently widely apart, the flagella again begin to move, carrying the organisms in a more diffuse stream once more to the surface. The whole culture vessel becomes filled with a series of vertical lines of closely aggregated falling organisms, surrounded by a broad cylinder of disseminated swimming ones, rising to the surface by the action of their flagella. If the conditions are kept uniform, such a circulation of *Euglenas,* falling to the bottom by gravity when the flagella are stopped and returning to the surface under their own power, will continue for days.

The flagellum in this species, therefore, retains its most primitive function of drawing the organism to the light in the surface layer. With the establishment of the flagellum an organ is produced which shows remarkable persistence in both the animal and vegetable kingdoms, and from the existence of the flagellated spermatozoon in the higher vertebrates, in accordance with Haeckel's biogenetic law that the individual in its development repeats or recapitulates the history of the race, we conclude that they also in their earliest history passed through a plankton flagellate phase.

Exactly at what stage in the history of the autotrophic flagellate the first formation of chlorophyll and its allied

pigments took place we have no means of determining, but it may have been before even the flagellum itself had begun. This advance and the subsequent concentration of the pigments into definite chromatophores or chloroplasts doubtless immensely increased the efficiency of the organism in producing the food which was necessary to it. The recent work of Baly and his collaborators becomes here again of the first importance, and though the subject of the part played by chlorophyll in photosynthesis belongs rather to botany and chemistry than to zoology, I may perhaps for the sake of completeness be allowed to refer to it very briefly. I have already said that Baly brought about the synthesis of formaldehyde from CO_2 and H_2O under the influence of rays of very short wave-length ($\lambda = 200\,\mu\mu$) from a mercury-vapor lamp. He was also able to show that when certain colored substances were added to the solution of carbon dioxide in water the same reaction took place under the influence of ordinary visible light. His explanation of this process is that the colored substance known as the photocatalyst absorbs the light rays and then itself radiates, at a lower infra-red frequency corresponding to its own molecular frequency, the energy it has absorbed. At this lower frequency the energy thus radiated is able to activate the carbonic acid, so that the reaction leading to the formation of formaldehyde can and does take place. In the living plant this synthesized formaldehyde probably at once polymerizes to form sugars.

Malachite green and methyl orange, as well as other organic compounds, were found to act as photocatalysts capable of synthesizing formaldehyde, and Moore and Webster's work had previously shown that inorganic substances, such as colloidal uranium oxide and colloidal ferric oxide, can do the same. Chlorophyll in living plants may with some confidence be assumed to operate in a similar way, though no doubt the series of events is more complex, since the green pigment itself is not a single pigment, and others, such as carotin and xanthophyll, are also concerned.

We have tried to picture the gradual building up from elements occurring in sea-water of a chlorophyll-bearing flagellate, capable of manufacturing its own nourishment and able to multiply indefinitely by the simple process of dividing in two. If we assume only one division during each night as a result of the day's work in accumulating food material, such an organism would be able in a comparatively short space of time to occupy all the natural waters of the world. But here we are met by a difficulty which is not easily overcome. Chlorophyll, the photocatalyst, the most essential factor in the building up of the new organic matter, is itself a highly complex organic substance, and in any satisfactory theory its original formation and its constant increase in quantity must be accounted for. Lankester[10] has maintained that chlorophyll must have originated at a somewhat late stage in the development of organic life, and has suggested that earlier organisms may have nourished themselves like animals on organic matter already existing in a non-living state. An alternative hypothesis, which in view of the recent work seems more attractive, is to suppose that the earlier organisms were either activated by some simpler photocatalyst, or that they received the necessary energy at suitable frequency directly from some outside source.

It must not be forgotten, also, that at the time these developments were taking place the conditions of the environment would in many ways have been different from those now existing in the sea. One suggestion of special interest that has been made[11] is that the concentration of carbon dioxide in the atmosphere, and hence also in natural waters, was very much greater than it is to-day. Free oxygen, indeed, may have been entirely absent, and all the free oxygen now present in the air may owe its existence to the subsequent splitting up of carbon dioxide by the action of plant life. With such possibilities of differences in the conditions in this and in so many

[10] "Treatise on Zoology," Part I, Introduction. London, 1909.

[11] See Carl Snyder, "Life without Oxygen," *Science Progress*, Vol. vi, 1912, p. 107.

other directions, may we not be well satisfied if, for the time, we can say that the formation of carbohydrates and proteids has been brought within the category of ordinary chemical operations, which can occur without the previous existence of living substance?

To return once more, however, to the free-swimming, autotrophic flagellate. In the early stages of its history the loss caused by sinking, and so getting below the influence of light and the possibility of further growth, must have been enormous. We may conceive a constant rain of dead and dying organisms falling into the darker regions of the sea, and thus a new field would be offered for the development of any slight advantages which particular individuals might possess. Under such conditions we may suppose that the holozoic or animal mode of nutrition first began in the absorption of one individual by another one, with which it had chanced to come into contact. If the one individual were more vigorous and the other moribund, we should designate the process "feeding," and the additional energy obtained from the food might well cause the individual to survive. If the two individuals which coalesced were both sinking from loss of vigor, the combined energy of the two might make possible a return to the upper water layers, where under the influence of light growth and multiplication would proceed, and we should, I suppose, designate the coalescence "conjugation," or sexual fusion.

Other individuals, again, sinking in shallow water, would stick to solid objects on the sea-floor, whilst the flagellum continued to vibrate. The current produced by the flagellum under these conditions would draw towards the organism dead and disintegrating remains of its fellows, and again we should have ingestion and animal nutrition. At this stage we witness the definite passage from plant to animal life. A further stage is seen when a cup-like depression to receive the incoming particles of food is formed at the base of the flagellum, to be followed still later by a definite mouth.

Any roughening of the external surface of the swim-

ming flagellate, such as we so often find brought about by the deposition of calcareous plates or silicious spicules or the production of ridges or furrows, would tend to slow down its speed of travel, from increased friction with the surrounding water. This would have a similar effect to actual fixation in drawing floating particles by the action of the flagellum, and also lead to animal nutrition. Still another development would occur when the fallen flagellate began to creep along the sea-floor by contractile movements of the plasmic surface, losing its flagellum, and adopting the mode of life of an amœba. That amœba and its allies, the Rhizopods, are descended from a flagellate ancestor is a view suggested by Lankester [12] in 1909, which was adopted by Doflein,[13] and is now strongly advocated by Pascher [14] as a result of much new research.

The transformation from the plant to the animal mode of feeding we can see in action by studying actual organisms which exist to-day. In the course of my work already referred to on the culture of plankton organisms there has on several occasions flourished in the flasks a small flagellate belonging to the group of Chrysomonads, which was first described by Wysotzky under the name of *Pedinella hexacostata,* and to which I drew the attention of Section D at the Cardiff Meeting in 1920. The general form of *Pedinella* resembles that of the common Vorticella, but its size is much smaller. The body, which is only about 5 μ in diameter, is shaped like the bowl of a wine glass, and from the base of the bowl, which is the posterior end, a short, stiff stalk extends. From the center of the anterior surface there arises a single long flagellum, surrounded at a little distance by a circle of short, stiff, protoplasmic hairs. Arranged in an equatorial ring just inside the body are six or eight brownish-green chromatophores or chloroplasts. In a healthy cul-

12 Lankester, "Treatise on Zoology," Part I, London, 1909, p. xxii.

13 Doflein, "Protozoenkunde," 1916.

14 Pascher, *Archiv f. Protistenkunde,* Bd. 36, 1916, p. 81, and Bd. 38, 1917, p. 1.

ture *Pedinella* swims about freely by means of a spiral movement of the flagellum, which functions as a tractor, the stalk trailing behind. The chromatophores are large, brightly colored and well developed, and the organism is obviously nourishing itself after the manner of a plant, like any other Chrysomonad. But from time to time a *Pedinella* will suddenly fix itself by the point of the trailing stalk. The immediate effect of this fixing is that a current of water, produced by the still vibrating flagellum, streams towards the anterior surface of the body, and small particles in the water, such as bacteria, become caught up on the anterior surface, the ring of fine stiff hairs surrounding the base of the flagellum being doubtless of great assistance in the capture of this food. One can clearly see bacteria and small fragments of similar size engulfed by the protoplasm of the anterior face of the *Pedinella* and taken into the body. The organism is now feeding as an animal. In some of the cultures in which bacteria were very plentiful nearly all the *Pedinella* remained fixed and fed in the animal way, and when this was so the chromatophores had almost disappeared, though they could still be seen as minute dark dots. We can, as it were, in this one organism see the transition from plant to animal brought about by the simple process of the freely swimming form becoming fixed.

In the group of Dinoflagellates, also—the group to which the naked and armored peridinians belong—the same transition from plant to animal nutrition can be well followed by studying different members of the group. In heavily armored forms, with a rich supply of chromatophores, nutrition is chiefly plant-like or holophytic. In those with fewer chromatophores there is, on the other hand, often distinct evidence of the ingestion of other organisms, and nutrition becomes partly animal-like. Amongst the naked Dinoflagellates such holozoic nutrition is very much developed, and in many species has entirely superseded the earlier method of carbonic acid assimilation.

It is really surprising how many structural features

found in higher groups of animals make their first appearance in these naked Dinoflagellates in conjunction with this change of nutrition, and we seem to be led directly to the metazoa, especially to the Cœlenterata. In *Polykrikos* there are well-developed stinging cells or nematocysts, as elaborately formed as those of Hydra or the anemones. In *Pouchetia* and *Erythropsis* well-developed ocelli are found, consisting of a refractive, hyaline, sometimes spherical lens, surrounded by an inner core of red pigment and an outer layer of black; the whole structure is comparable to the ocelli around the bell of a medusa. In *Noctiluca* and in the allied genus *Pavillardia* a mobile tentacle, which is doubtless used for the capture of food, is developed. Division of the nucleus, with the formation of large, distinct chromosomes, has also been described in several of these Dinoflagellates. With the tendency of the cells in certain species to hold together after division and form definite chains, we seem to approach still nearer to the metazoa, until, finally, in *Polykrikos* we reach an organism which may well have given rise to a simple pelagic cœlenterate. It is difficult to resist the suggestion put forward by Kofoid[15] in his recent monograph, that if to *Polykrikos,* with its continuous longitudinal groove which serves it as a mouth, its multicellular and multinucleate body and its nematocysts, we could add the tentacle of *Noctiluca,* and perhaps also the ocellus of *Erythropsis,* "we should have an organism whose structure would appear prophetic of the Cœlenterata and one whose affinities to that phylum and to the Dinoflagellata would be patent." Or it may be that the older view is the correct one here, and that the first cœlenterate came from a spherical colony of simple holozoic flagellates, arranged something on the plan of *Volvox,* in which the posterior cells of the swimming colony, in whose wake food particles would collect, had become more specialized for nutrition than the rest.

Before proceeding, however, to consider the further

[15] Kofoid and Swezy, "The Free-living Unarmored Dinoflagellata." Mem. Univ. California, 1921.

progress of animal life, we must pause for a moment to ask in what direction plant life in the sea developed, from which the increasing animal life derived its nourishment. Here the striking fact is the lack of progress in the free, floating, plankton phase. The plant life of the plankton has never proceeded beyond the unicellular stage, for the plankton diatoms, which with the peridinians form the great, fundamental vegetable food supply of the sea, are only autotrophic flagellates which have lost their flagella, having acquired other means of flotation to keep them in the sunlit region of the upper water layers. Deriving their food, as these plants do, directly from molecules in the sea-water, the factor which is for them of supreme importance is the exposure of maximum surface directly to the water. Hence the minute unicellular form has been the only one to survive as phytoplankton. The marine region in which plant life has succeeded in making some progress is the narrow belt along the shores, where a fixed life is possible, but this belt, limited by the amount of light which penetrates, extends only to a depth of about 15 fathoms. The available area is further restricted to rocky and hard bottoms, and is therefore nowhere great. This is the wave-lashed region of the brown and red seaweeds. In the brown seaweeds a history can still be traced,[16] from the fixture of an autotrophic flagellate to the building up, by laying cell on cell, of the essential structures which afterwards, on transmigration to the land, reached their climax in the forest tree.

But if the flagellate thus rose and gave origin to the flora of the land, it also degenerated, for it adopted a parasitic habit, living in and directly absorbing already formed organic matter. In this way the bacteria arose, whose activities in so many directions influence the life of to-day. This view exceeds in probability, I think, the suggestion often put forward,[17] that it is to the simpler bacteria we must look for the first beginnings of life.

16 Church, *Botanical Memoirs,* No. 3. Oxford, 1919.

17 Osborn, "The Origin and Evolution of Life," 1918. Waksman and Joffe, "Micro-organisms concerned in the Oxidation of Sulphur in the

After this digression on the botanical side we must return to the primitive cœlenterate and see on what lines evolution proceeded in the animal world. As a purely plankton organism, swimming freely in the water, the progress of the cœlenterate was not great, and reached, as far as we know, no further than the modern Ctenophore. The Ctenophore seems to represent the culminating point of the primary progression of pelagic animals, which derived directly from the autotrophic flagellate. Further evolution was associated with an abandonment by a cœlenterate-like animal of the pelagic habit, and the establishment of a connection with the sea bottom, either by fixing to it, by burrowing in it, or by creeping or running over it. At a later stage many of the animals which had become adapted to these modes of life developed new powers of swimming, and thus gave rise to the varied pelagic life which we find in the sea to-day; but this must be regarded as secondary, the primary pelagic life, so far as adult animals were concerned, having ended with the evolution of the Ctenophore.[18] Such is the teaching of embryology, the history of the race being conjectured from the development of the individual. In group after group of the animal kingdom, when the details of its embryology become known, the indications are the same—first the active spermatozoon, reminiscent of the plankton flagellate, then the pelagic larval stage, recalling the cœlenterate, and then a bottom-living phase.

The primitive, free-swimming cœlenterate, adopting a fixed habit and becoming attached mouth upwards to solid rock or stone, gave rise to hydroids, anemones and

Soil,'' *Journal of Bacteriology,* VII, 2, March, 1922. The authors claim that *Thiobacillus thiooxidans* will grow in solutions containing no organic matter. In view of the minute traces of organic matter that suffice for the growth of bacteria and molds, care must be taken, however, in drawing conclusions from experiments made in flasks or tubes closed in the ordinary way with cotton-wool plugs and subsequently sterilized in flowing steam.

[18] There is perhaps a possibility that further knowledge of the embryology of Sagitta and its allies might make it necessary to modify this suggestion.

corals, typical inhabitants of the coastal waters, for the sands and muds at greater depths offered few points of attachment sufficiently stable.

A Volvox-like colony of simple holozoic flagellates, according to MacBride,[19] commenced to feed upon microscopic organisms lying on the sea bottom, and under these circumstances only the cells of the lower half of the colony would be effective feeders. The upper cells, therefore, lost their flagella and became merely a protective layer, which finally grew downwards outside the others and fixed the colony to the ground. In this way a sponge was formed. The collar cell, so typical of the group, had been developed already by the flagellates, its first inception being perhaps a circle of protoplasmic hairs such as we find in *Pedinella*. But this adoption of a fixed habit, as it were mouth downwards, did not lead very far, and though there has been much elaboration within the group itself, the sponges have remained an isolated phylum, unable to develop into higher forms.

It is in a Ctenophore-like ancestor that we find the line of development to higher animal groups, and this ancestor must have been at one time widely distributed in the seas. Its immediate descendants are familiar to every zoological student in the well-known series of pelagic larval forms. Müller's larva, taking to the bottom, and in its hunt for food gliding over hard surfaces with its cilia, led to the flatworms; the *Pilidium*, developing a thread-like body and creeping into cracks and crevices to transfix its prey, gave rise to the nemertines. A Trochophore, burrowing in soft mud and sand, developed a segmented body which gave it later the power of running on these soft surfaces, and became an annelid worm. Another Trochophore, developing a broad, muscular foot, crept on the sand, and afterwards buried itself beneath it as a lamellibranchiate mollusc, or migrated on to harder surfaces as the gastropod and its allies. *Pluteus*, *Bipinnaria*, *Auricularia*, first fixing, as the crinoids still do, and developing a radial symmetry, afterwards broke free and wandered on the bottom as sea-urchin, star-fish

[19] "Textbooks of Embryology. Invertebrata." London, 1914.

and cucumarian. *Tornaria* developed into *Balanoglossus,* whose structure hints to us that the ascidians and vertebrates came from a similar stock. All the phyla thus represented derive directly from the free-swimming Ctenophore-like ancestor, and only one considerable group, the Arthropods, remains unaccounted for. The evolutionary history of an Arthropod is, however, not in doubt. Its marine representatives, the Trilobites and Crustacea, came directly from annelids, which, after their desertion of a pelagic life to burrow in the sea-floor and run along its surface, again took to swimming, and not only stocked the whole mass of the water with a rich and varied life of Copepods, Cladocera and Schizopods, but gave rise to Amphipods, Isopods, and Decapods, groups equally at home when roaming on the bottom or swimming above it.

Another important addition to the pelagic fauna we should also notice here. From the molluscs, creeping on solid surfaces, sprang a group of swimmers, the Cephalopods, which have grown to sizes almost unequaled amongst the animals of the sea.

All these invertebrate phyla had become established and most of them had reached a high degree of development in the seas of Cambrian times. Amongst animals then living there are many which have survived with little change of form until to-day. One is almost tempted to suggest that the life which the sea itself could produce was then reaching its summit and becoming stabilized. Since Cambrian times geologists tell us some thirty million years [20] have passed, a stretch of time which it is really difficult for our imaginations to picture. During that time a change of immense moment has happened to the life of the sea; but if we read the signs aright, that change had its origin rather in an invasion from without than in an evolution from within. Whence came that tribe of fishes which now dominates the fauna of the sea? It would be rash to say that we can give any but a speculative reply to the question, but the probable answer seems to be that fishes were first evolved not to meet

[20] Osborn, "Origin and Evolution of Life," 1918, p. 153.

conditions found in the sea, but to battle with the swift currents of rivers, where fishes almost alone of moving animals can to this day maintain themselves and avoid being swept helplessly away.[21] It was in response to these conditions that elongate, soft-bodied creatures, which had penetrated to the river mouth, developed the slender, stream-lined shape, the rigid yet flexible muscular body, the special provision for the supply of oxygen to the blood to maintain an abundant stock of energy, and all those minute perfections for effective swimming that a fish's body shows. The fact that many sea-fishes still return to the rivers, especially for spawning, supports this view, and it is in accordance with Traquair's classical discoveries of the early fishes of the Scottish Old Red Sandstone, which were for the most part fresh- and brackish-water kinds.

Having developed, under the fierce conditions of the river, their speed and strength as swimmers, the fishes returned to the sea, where their new-found powers enabled them to roam over wide areas in search of food, and gave them such an advantage in attack and defense that they became the predominant inhabitants of all the coastal waters, and as such they remain to-day.

The other great migration of the fishes, also, the migration from the water to the land, giving rise to amphibians, reptiles, birds and mammals, must not be left out of account. The whales, seals and sea-birds, which after developing on land returned again to the waters and became readapted for life in them, are features which can not be neglected.

And so we are brought to the picture of life in the sea as we find it to-day. The primary production of organic substance by the utilization of the energy of sunlight in the bodies of minute unicellular plants, floating freely in the water, remains, as it was in the earliest times, the feature of fundamental importance. The conditions which control this production are now, many of them, known. Those of chief importance are (1) the amount of light which

21 Chamberlin, quoted in Lull, "Organic Evolution," New York, 1917, p. 462.

enters the water, an amount which varies with the length of the day, the altitude of the sun, and the clearness of the air and of the water; (2) the presence in adequate quantity of mineral food substances, especially nitrates and phosphates; and (3) a temperature favorable to the growth of the species which are present in the water at the time. Experiments with cultures of diatoms have shown clearly that if the food-salts required are present, and the conditions as to light and temperature are satisfactory, other factors, such as the salinity of the water and the proportions of its constituent salts, can be varied within very wide limits without checking growth. The increased abundance of plankton, especially of diatom and peridinian plankton, in coastal waters and in shallow seas largely surrounded by land, such as the North Sea, is due to the supply of nutrient salts washed directly from the land by rain or brought down by rivers. An exceptional abundance of plankton in particular localities, which produces an exceptional abundance of all animal life, is also often found where there is an upwelling of water from the bottom layers of the sea. These conditions are met with where a strong current strikes a submerged bank, or where two currents meet. Food-salts which had accumulated in the depths, where they could not be used owing to lack of light, are brought by the upwelling water to the surface and become available for plant growth. The remarkable richness of fish life in such places as the banks of Newfoundland and the Agulhas Banks off the South African coast, each of which is the meeting-place of two great currents, is to be explained in this way.

Our detailed knowledge of the steps in the food-chain from the diatom and peridinian to the fish is increasing rapidly. The Copepod eats the diatom, but not every Copepod eats every diatom; they make their choice. The young fish eats the Copepod, but again there is selection of kind. Even adult fishes like herring and mackerel, which were formerly supposed to swim with open mouth, straining out of the water whatever came in their way, are now thought largely to select their food.[22]

[22] Bullen, *Journ. Mar. Biol. Assoc.*, 9, 1912, p. 394.

A result of extraordinary interest in connection with the food-chain has recently been brought to light by two sets of investigators working independently. In seeking to explain certain features which he had found in connection with the growth of the cod, Hjort[23] undertook a study of the distribution in marine organisms of the growth stimulant known as vitamin. Fat-soluble vitamin was already known to be present in large quantities in cod-liver oil, and is what probably gives the oil its medicinal value. Hjort was able to trace the vitamin, by means of feeding experiments on rats, in the ripe ovaries of the cod, in shrimps and prawns, which resemble the animals on which the cod feeds, and in diatom plankton and green algæ. Jameson, Drummond and Coward[24] cultivated the diatom *Nitzschia closterium,* and by a similar method to that used by Hjort showed that it was extraordinarily potent as a source of fat-soluble vitamin. We thus conclude that this substance, so essential to healthy animal growth, is produced in large quantities by plankton diatoms, and passed on unchanged to the fish through the crustaceans which feed on the diatoms. In the fish the vitamin is first stored in the liver, and with the ripening of the ovary passes into the egg, to be used to stimulate the growth of the next generation. Again we see the fundamental importance of the food-producing activities of the lowest plant life.

Attention has already been drawn to the suggestion that fishes developed their remarkable swimming powers in rivers, in response to a need to overcome the currents, and that they afterwards returned to the sea, where they preyed upon a well-developed and highly complex invertebrate fauna already fully established there. Their speed enabled them to conquer their more sluggish predecessors, whilst they themselves were little open to attack. With the exception of the larger cephalopods, which are of comparatively recent origin, and were probably evolved after the arrival of the fishes, there are few, if any, invertebrates which capture adult fishes as part of their

23 *Proc. Roy. Soc.,* May 4, 1922.

24 *Biochemical Journal,* 1922.

normal food. Destructive enemies appeared later in the form of whales and seals and sea-birds, which had developed on the land and in the air.

And now in these last days a new attack is made on the fishes of the sea, for man has entered into the struggle. He came first with a spear in his hand; then, sitting on a rock, he dangled a baited hook, a hook perhaps made from a twig of thorn bush, such as is used to this day in villages on our own east coast. Afterwards, greatly daring, he sat astride a log, with his legs paddled further from the shore, and got more fish. He made nets and surrounded the shoals. Were there time we might trace step by step the evolution of the art of fishing and of the art of seamanship, for the two were bound up together till the day when the trawlers and drifters kept the seas for the battle fleet.

There can be little doubt that in European seas the attack on the fishes in the narrow strip of coastal water where they congregate has become serious. A considerable proportion of the fish population is removed each year, and human activity contributes little or nothing to compensate the loss. We have not, however, to fear the practical extinction of any species of fish, the kind of extinction that has taken place with seals and whales. Fishing is subject to many natural limitations, and when fishing is suspended recovery will be rapid. There is evidence that such recovery took place in the North Sea when fishing was restricted by the War, though the increase which was noted is perhaps not certainly outside the range of natural fluctuations. Until the natural fluctuations in fish population are adequately understood, their limits determined, and the causes which give rise to them discovered, a reliable verdict as to the effect of fishing is difficult to obtain.

If such problems as these are to be solved, the investigation of the sea must proceed on broadly conceived lines, and a comprehensive knowledge must be built up, not only of the natural history of the fishes, but also of the many and varied conditions which influence their lives. The life of the sea must be studied as a whole.